No. 6. — *The Nervous System of Nereis virens Sars. A Study in Comparative Neurology.* By J. I. Hamaker.[1]

CONTENTS.

INTRODUCTION.

Although so much has been written on the nervous system of representatives of all the chief groups of the metazoa, we are as yet far from thoroughly understanding the action of the myo-neural mechanism of any animal. It is true, much light has been thrown upon the subject during the last decade through the use of the newer methods of investigation; but the many valuable facts that have been established are as yet so disconnected, that they can scarcely be said to be more than suggestive. In no case has the myo-neural system of an animal been at all completely worked out. In the higher animals the complexity of this system makes such a task almost impossible. At any rate, the most

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promising method of approaching the subject would seem to be through the simpler forms. Some of the homodynamously segmented animals offer advantages in this respect which no other forms do.

The following considerations may be noted as applying particularly to the polychæte annelid, Nereis, as a favorable subject for this kind of study:—(1) Nereis has a sharply centralized nervous system, consisting of well defined ganglia, which occupy very definite relations to the parts they control. (2) The histological elements of the nervous system are highly differentiated and constant in their relationships. (3) A typical body segment of the animal is simple in structure, having a comparatively small number of muscles. (4) There is almost no serial differentiation of the body segments, excepting in a few of the anterior and the anal metameres; hence it is necessary to determine the structure of one segment only in order to know the structure of nearly the whole animal. (5) Since there are only a few muscles, the movements of the animal are limited in number, and may readily be analyzed and classified. (6) Physiological experiments may be performed with more than usual facility, because the worms are hardy and live well in the aquarium. To these considerations may be added the eminently practical one that Nereis may be easily obtained in unlimited quantities. With such material the problem before us seems to be presented in a comparatively simple form. By these considerations I was led to take up the study of the nervous system of Nereis. Some of the results obtained are given in what follows.

Methods.

The material used for intra-vitam staining was the atokal form of Nereis virens Sars. It was obtained from the muddy banks of the Charles River at a place where the water at low tide contains less than 0.3% salt. The worms found here may be transferred to fresh water without suffering serious injury. For ordinary histological preparations both atokal and epitokal forms were used. The latter were obtained from the mud flats of Lynn Harbor at the mouth of the Saugus River.

Before killing, the specimens were narcotized with chloral hydrate or alcohol, and the intestine cleaned by forcing a stream of water through it. The body was always opened to allow rapid penetration, and sometimes the intestine was removed. Two methods of fixing and staining were employed: either fixing in corrosive sublimate and staining in iron-hæmatoxylin, or fixing and staining by osmic acid. The value of corrosive sublimate as a fixing agent is well known, and I obtained excellent

results by fixing in a 1% to 5% solution of acetic acid saturated with corrosive sublimate. Preparations fixed in this way were stained on the slide with Heidenhain's iron-hæmatoxylin. The osmic acid method of vom Rath ('95) gives results in many ways equally good, and for some purposes, such as tracing nerves, even better than the corrosive and iron-hæmatoxylin method. I found a mixture in the following proportions of osmic acid, picric acid, acetic acid, and platinic chloride very satisfactory: —

Osmic acid, 2%	12 c.c.
Picric acid, sat. aq. sol.	100 c.c.
Platinic chloride, 2%	25 c.c.
Acetic acid	1 c.c.

The results obtained are not at all uniform in quality, since the rate of precipitation of the osmium by the pyroligneous acid seems to vary. The value of successful preparations, however, counterbalances the capriciousness of the method. The results obtained by these two methods agree in almost every particular, even to the relative intensity of the stains in the various tissues.

For intra-vitam staining the following method proved most successful. Specimens of Nereis having about seventy segments were injected with a concentrated solution of methylen blue in normal salt solution. They were then laid, ventral side uppermost, in a moist chamber for about two hours, after which the stain began to appear in the sub-œsophageal ganglion. From this region the stain gradually penetrated caudad, and when it was thought to have reached its optimum, it was fixed by Bethe's ('95) ammonium molybdate method. The objects were then embedded in paraffine and cut.

PART I. DESCRIPTION.

1. Topography.

The central nervous system of Nereis virens is well developed. Throughout the entire length of the body the ventral nerve cord exhibits a sharp differentiation of ganglia and longitudinal connectives. The ganglia are segmentally arranged and constant in position; the nerves are regularly arranged in metameric groups of five pairs each (Plate **1**, Fig. 8). The ventral cord lies deeper than the hypodermis, from which it is partially separated by the circular muscle bundles.

The circular muscles do not form a continuous sheet, but consist of small bundles which lie partially embedded in the hypodermis. Some of these muscles cross the mid-ventral line external to the nerve, thus causing a partial separation of cord and hypodermis. Between the muscle bundles, however, the neurilemma of the nerve cord is in contact with the hypodermis. The brain also lies deeper than the hypodermis, from which it is suspended by a narrow membrane lying in the median plane.

a. Brain.

The form of the brain is roughly that of a trapezoid (Plate 1, Fig. 1, *ceb.*), the anterior pair of eyes marking approximately the extremities of the longer one of the parallel sides, while the posterior pair marks the limits of the shorter one. The anterior angles of the trapezoid are drawn out toward the palps, thus making the anterior margin of the brain slightly concave. The dorsal aspect of the brain is broadly cordate, the re-entrant angle being at the anterior side. Fourteen pairs of nerves arise from the brain by distinct roots. As they are arranged symmetrically, it will not be necessary to describe both sides. Beginning anteriorly at the median line, and numbering and describing the nerves of one side in order, there is first near the median line a group of three nerves (I, II, III), which arise near together.

The first nerve (I) passes forward, then downward, and finally backward along the dorsal wall of the proboscis; the second (II) goes directly forward to the antenna; the third (III) runs forward along the dorsal wall of the head.

At the anterior lateral angle of the brain there is another group of three nerves (IV, V, VI). The fourth nerve (IV) divides into two branches, one going to the ventro-median wall of the palp, the other to the dorso-median wall of the same organ. The fifth nerve (V) extends ventrally to the proboscis; the sixth (VI) is the large sensory trunk of the palp; and the seventh (VII) arises from the brain laterally, between the group just described and the anterior eye of the same side; it passes forward along the lateral wall of the palp.

The eighth, ninth, and tenth nerves are the three roots of the circumœsophageal commissure. They unite in the commissural ganglion, which lies a short distance ventral to the anterior eye. The eighth (VIII) is a small nerve arising near the seventh, passing out parallel with it, and then turning down into the ganglion. The ninth nerve (IX) arises laterally from the brain, passes out directly beneath the eye, and then bends down to the commissural ganglion. The tenth (X) arises from the

ventral edge of the brain immediately ventral to the ninth, and passes out directly to the commissural ganglion.

The eleventh (XI) and twelfth (XII) nerves are the two optic nerves. They converge from the eyes toward the centre of the brain.

The thirteenth (XIII) nerve arises back of the posterior eye, and goes directly to the ciliated groove. The fourteenth (XIV) is a rather diffuse nervous connection between the brain and the dorsal surface of the head. The region innervated lies nearly midway between the posterior eye and median plane, but slightly nearer the latter.

Besides these fourteen paired nerves (I–XIV) there is a single median nervous connection between the dorsal surface of the head and the brain. This is similar to the diffuse fourteenth nerve, but is smaller and lies slightly anterior to it. Its position is shown in Figure 1.

From the commissural ganglion a nerve (α) passes forward to the proboscis, where it unites with the fifth nerve of the brain (V) in a ganglion. Another nerve (δ) passes backward along the side of the head. Four or five small connectives, not shown in Figure 1, unite the commissural ganglion with the optic ganglion, which lies in contact with the ventral side of the anterior eye. Lastly, the circum-œsophageal commissure passes from the commissural ganglion around the œsophagus to the sub-œsophageal ganglion, traversing on its way a ganglion which lies beneath the anterior pair of tentacular cirri. From this anterior cirrus ganglion two large nerves go each to an anterior cirrus, and, from the anterior side of it, a smaller one (β) to the proboscis. On its posterior side the anterior cirrus ganglion is connected by a small nerve (θ) with the posterior cirrus ganglion, which lies beneath the posterior pair of tentacular cirri. The latter ganglion gives off two large nerves, one to each of the two posterior tentacular cirri, and also sends a nerve (ζ) backward along the side of the head. The posterior cirrus ganglion is connected with the sub-œsophageal ganglion by a large nerve trunk (*n. pa-coms.*), which lies posterior to and parallel with the circum-œsophageal commissure. This trunk gives off several branches from a region midway between the posterior cirrus ganglion and the sub-œsophageal ganglion.

b. Sub-œsophageal Ganglion.

The sub-œsophageal ganglion (*gn. sb-oe.*, Fig. 1) lies on the posterior boundary of the cephalic segment. It gives off three pairs of nerves besides the commissures and the nerves of the posterior cirri. Begin-

ning at the median plane, the first pair of nerves (γ) goes to the œsophagus; they pass forward near the median line, and then bend backward to be distributed to the ventral wall of the œsophagus. The second and third pairs are respectively the commissures and the nerves of the posterior cirri; the other two pairs pass out laterally and forward to the walls of the cephalic segment. The ganglia of the first three or four body segments are displaced backward, as compared with those of the typical segment, and are consequently crowded together, thus making them appear as a single ganglion. Each segment in this region receives the typical number of nerves, though in regard to size the nerves of each segment do not bear quite the same relation one to another as they do in a typical segment.

c. Typical Body Segment.

The ganglia of the ventral chain (Plate **1**, Fig. 8) are about half as long as the segment, and, if the segmentation of the longitudinal musculature be taken to indicate the boundaries of the metameres, they lie intersegmentally, with at least two thirds their length in the posterior segment. The longitudinal connectives are enclosed in a single sheath, so that there appears to be but one connective. At the intersegmental plane there is a constriction of the investing tissue of the ganglion, but this does not extend to the nervous part. Five larger pairs of nerves are given off from each ganglion, and there are, besides, many smaller ones, which consist of only a few fibres each. A few of the latter are given off ventrally, but most of them pass dorsally from the mid-dorsal line of the nerve cord, and probably are distributed chiefly to the digestive tube.

The paired nerves are most conveniently characterized with reference to their position in the segment. Beginning at the anterior end, there is close behind the intersegmental constriction of the ganglion the first segmental nerve (I, Fig. 8). This nerve is rather slender and passes out at right angles to the ventral nerve cord. It lies external to the longitudinal muscles, and is partly buried in the hypodermis (I′, Fig. 4). It may be traced with little change in calibre to the dorsal base of the parapodium, where it is lost either in the circular parapodial muscles, or in the hypodermal plexus, or most likely in both.

The second segmental nerve (II) is the largest of the five, and is the parapodial trunk. It leaves the segmental ganglion near its posterior end and passes diagonally backward across and external to the longi-

tudinal muscles to the parapodial ganglion, which lies in the ventral base of the parapodium between the longitudinal muscles and the pore of the segmental organ.

The third segmental nerve (III) is very small. It arises from the posterior end of the segmental ganglion and passes diagonally outward and backward to the posterior base of the parapodium. Like all the paired segmental nerves, it lies embedded in the hypodermis throughout its length. Next in size to the parapodial trunk is the fourth nerve (IV). It arises from the anterior third of the succeeding ganglion, and hence lies in the posterior part of the segment, near the intersegmental line, where the longitudinal muscles are attached to the hypodermis. It runs parallel with the first nerve (I) of the following segment, but continues in a direct course around the body almost to the mid-dorsal line.

The fifth segmental nerve (V) is very slender. It lies close behind the fourth nerve, and very near the intersegmental plane. It extends as far as the base of the parapodium.

d. Parapodial System.

The innervation of the parapodium (Figs. 5, 8) is almost wholly from the parapodial ganglion, from which four nerves radiate toward the periphery. The most anterior one (1) is very slender and usually passes out in front of the pore of the segmental organ. It goes to the retractor muscles of the anterior side of the parapodium. The second parapodial nerve (2) is comparatively large, and innervates the ventral ramus. Near the ganglion it divides into an anterior and a posterior branch. The anterior one passes along the anterior wall of the ventral ramus to the anterior setigerous lobe. The other runs along the posterior wall to the posterior setigerous lobe, giving off a branch to the ventral cirrus and another to the inferior ligula of the ventral ramus.

The third parapodial nerve (3) passes outward and upward on the posterior wall of the parapodium. About half way up the side of the parapodium it gives off a branch to the glandular region of the dorsal base of the parapodium. Then other branches are sent to the anterior setigerous lobe of the dorsal ramus, the posterior setigerous lobe, the superior ligula, and the dorsal cirrus.

A fourth parapodial nerve (4) goes to the posterior base of the parapodium.

2. Protective Tissue.

The protective tissue of the central nervous system is of two kinds; an outer membrane, the neurilemma, and within this a spongy tissue, the neuroglia. The neurilemma is better developed in the anterior than in the posterior region of the animal, and better in the older epitokal individuals than in the atokal forms. In the cephalic segment it is very thick and forms a capsule around the brain (*n'lem.*, Plate **2**, Fig. 9), and it also envelops the nerves from the brain. A tissue similar in texture lines the dorsal wall of the head, there taking the place of a basement membrane (Plate **3**, Fig. 20). The brain capsule is continuous with this lining of the wall of the head along the mid-dorsal line, and also around the nervous connections that unite the brain with the posterior dorsal surface of the head. It likewise serves as a place of attachment for some of the muscles of the head, as the neurilemma of the ventral cord does for some of the diagonal muscles; but elsewhere the capsule is free from the wall of the head, being suspended in the cavity of the cephalic lobe.

The neurilemma of the brain is continuous with that of the ventral cord along the circum-œsophageal commissures. Except where it is pierced by nerves, the neurilemma of the cord (Plate **2**, Fig. 18) forms a closed tube, whose walls are thickest at the anterior end. Along its dorsal side the wall of the neurilemma tube is continuous with the tunica intima of the ventral longitudinal blood-vessel by means of a narrow membrane which connects the two tubes throughout their entire lengths (Fig. 18).

In structure the neurilemma is uniformly fibrous; it does not stain in iron-hæmatoxylin or osmic acid. On the outer surface of the brain capsule there is a layer of nuclei which may possibly belong to the neurilemma. I have not clearly seen such nuclei on the neurilemma of the ventral cord. The connective tissue of the muscles is continuous with the neurilemma in many places, and resembles it in every respect.

The neuroglia of the brain is a network of delicate fibres with numerous small elongated nuclei located at the nodes of the network. This tissue lines the inner surface of the brain capsule, from which it penetrates into all parts of the brain except the neuropil and the masses of small nuclei connected with it. The neuroglia of the ventral cord is like that of the brain in texture, and it surrounds and penetrates the nervous structures of the cord in the same way as in the brain. The portion immediately surrounding the cord, however, is somewhat differentiated

from the more peripheral part (Plate **2**, Fig. 18). Its fibres are coarser and more compact, and they take a circular direction around the cord. Between the successive ganglia the fibres of this inner layer also pass in between the three longitudinal connectives. A few neuroglia nuclei lie scattered about among the nerve fibres of the cord.

3. Brain.

The brain of Nereis consists essentially of a central mass of interwoven fibres with a few irregular masses of neuropil, and a peripheral layer of cells loosely arranged in symmetrical groups. The cells have undergone a remarkable degree of differentiation, and the cells in each pair of groups have distinct characteristics. There are at least six distinct classes of cells; while a number of the larger cells are arranged symmetrically in pairs, each pair having individual peculiarities of form and structure. The six classes, however, are not characterized by form and structure alone. Indeed, it is the difference in chemical reaction that is most distinctive, and calls for more than passing mention. The classes are as follows: —

(1) In front, on each side of the brain, between the anterior median and the anterior lateral groups of nerves, there lie two masses of exceedingly small nuclei (Plate **3**, Figs. 21, 24). The larger ventral mass is approximately crescentic in a transverse section of the brain with the concave side of the crescent lateral and partially embracing a mass of neuropil. The smaller, dorsal mass of cells is also crescentic in transverse section, but with the concave side toward the median plane. This crescent also partially embraces a mass of neuropil. In preparations stained with osmic acid or iron-hæmatoxylin the cells of these masses show only very faint traces of cell boundaries. The nuclei stain very deeply, and always contain a number of granules of various sizes. The nuclei are about 6μ in diameter and are arranged in rows radiating from the neuropil (Fig. 21). They are set very closely in the rows, and are often almost in contact. The spaces between the rows are wider toward the neuropil, while toward the convex side of the mass the arrangement is more compact and the alignment of the nuclei almost disappears. The spaces between the rows of nuclei have a fine fibrous appearance, as though fibres from the cells passed out to the neuropil. Cells similar to these occur in other parts of the brain, e. g. a small group at the posterior border of the brain, just median to the root of the nerve which runs to the ciliated groove (XIII). Cells slightly larger, but otherwise like

these, occur scattered over the dorsal surface of the brain, and a group of them lies around the root of the fourteenth nerve (XIV).

(2) At the posterior lateral border of the brain there is a group of spindle-shaped cells, which extends backward and outward along the root of the thirteenth nerve (XIII) as far as the point where the nerve pierces the capsule (Plate **2**, Figs. 9, 15). These cells do not stain very deeply, and do not show very sharply defined cell boundaries, although the spindle form can be distinctly seen. Similar cells give rise to the fibres that form the fourteenth nerve and pass out to the dorsal surface of the head.

(3) Along the internal border of the last group there lies a third very peculiar class of cells (Figs. 9, 12). Unlike those of the two preceding classes, the cells of this class have a very definite cell boundary. They are comparatively few in number, and are narrowly pear-shaped with the process extending toward the centre of the brain. In preparations stained to best advantage for other structures these cells are so deeply stained that only in a few cases can the nucleus of the cell be seen at all. The cell process also stains so deeply that it appears in strong contrast with the other fibres.

(4) In the same transverse section as the last, but nearer the median plane, is another group of pear-shaped cells (Figs. 9, 11). These are larger and proportionately broader than the last, and stain very differently from them. In iron-hæmatoxylin the cytoplasm does not become blue, but takes on a brownish color. Its structure is almost homogeneous excepting an irregular network of a few coarse fibres which usually centres about the nucleus and does not extend throughout the body of the cell. The processes of these cells also go toward the centre of the brain.

(5) At the side of the brain beneath the nerve of the anterior eye there lies a group of cells which seem to have no direct connection with the brain except that of being enclosed in the brain capsule. The cells are rather large and spherical, and send their processes out along the ninth nerve (IX) of the brain toward the commissural ganglion. A few of the cells lie scattered along the dorsal side of the ninth nerve, and make this group of cells continuous with the group which lies beneath the anterior eye, and which we have called the optic ganglion. The cells of both groups have the same general appearance (Fig. 19). The cytoplasm presents no special peculiarities. There is no cell membrane and the limits of the cell are very indistinct, because there are very few granules at the periphery. Each cell is surrounded by neuroglia fibres

arranged loosely in concentric layers. The inner fibres seem to be embedded in the cytoplasm of the cell.

(6) Although the remaining cells (Figs. 16, 17) present a great variety of size, form, and detail of structure, there is a general similarity which permits of classing them together as a group distinct from those we have described thus far. They have the pear shape and the granular cytoplasm which are characteristics of most of the cells of the ventral ganglia. But beyond this there is little that is common to all the cells of the group. In the posterior half of the brain there are several pairs of very large cells which have the characteristics of this group, and in addition a very striking one of their own. The nucleus lies in the narrow end of the cell, and is surrounded by the granular cytoplasm. At the other end of the cell, there is a large vacuolar space containing a number of deeply staining bodies of irregular form, embedded in an indistinct coagulum. Other cells have very finely granular substance occupying a similar position, the granules being much smaller and staining less deeply than those of the body of the cell. In these cases the nucleus shows no signs of degeneration. In some cells (Fig. 16) the cortical part of the cytoplasm is penetrated by narrow lamellæ, which, when viewed from the surfaces of the cell, present the appearance of a honeycomb structure.

There is another structure within the brain capsule which is very strange, and for which I cannot account. It consists of a considerable number of spheroidal cavities (Fig. 10), containing a substance which assumes several forms. The cavities are arranged in two symmetrical groups, one on each side of the brain (Fig. 9), extending around and between the fibres of the fourteenth nerve, and backward and outward to the root of the thirteenth nerve. The cavities, which are surrounded by neuroglia, vary somewhat in size, the average being about equal to that of the average nerve cell of the brain. Each usually contains a number of spherical granules, sometimes of nearly uniform size, sometimes differing much in this respect. They are stained in iron-hæmatoxylin, but in preparations treated with osmic acid they are yellow. Sometimes the cavities are filled with an almost homogeneous substance; at other times, however, the substance only partially fills the cavities, and assumes an irregular stellate form. In a few cases there are doubtful indications of a nucleus.

These structures cannot be due to degeneration of nerve cells, because they are very regular in the place of their occurrence, and there is no indication of degenerated fibre tracts. The contents of the cavities are

not fat, for they are not blackened by osmic acid, nor do they seem to be pigment, since the granules are comparatively large and at the same time quite variable in size. Racowitz ('95) found amœboid cells depositing pigment in the region of the ciliated groove, but I have no reason to think the condition in the present instance is due to the same instrumentality.

4. Ciliated Groove.

The ciliated grooves lie on the posterior margin of the cephalic lobe behind the posterior eyes (Plate **3**, Fig. 20). A fold of the anterior margin of the cephalic segment extends forward a short distance over the cephalic lobe, to which it is attached in the median plane, and also at a point just lateral to the eyes. On the ventral wall of the pockets thus formed there is an elongate eminence or ridge about 0.5 mm. long and 0.2 mm. wide, with the long axis transverse to the body. Along the crest of this ridge lies the ciliated groove. The ridge is formed by a thickening of the non-ciliate hypodermis, the cells of which are very long and arranged with their distal ends directed toward the crest of the ridge, thus producing in cross section the figure of an inverted V. The space between the cells which form the ridge is occupied by the ciliated cells. The cuticula over these cells is very thin, and the cilia project through it, forming a narrow band along the bottom of the groove. The nuclei of the ciliated cells lie much deeper than those of the non-ciliate cells on either side of them. The organ is innervated by the nerve XIII. There are no glands in the hypodermis of this region, but the overhanging fold of the cephalic segment is richly supplied with them.

5. Ventral Nerve Cord.

The structure of the ventral nerve cord can best be set forth by describing transverse and longitudinal sections of it. A transverse section between ganglia (Plate **5**, Fig. 31) shows that there are three longitudinal connectives; two large lateral and symmetrical ones, and a small, more dorsal median one. Each connective is enveloped by the fibres of the inner layer of neuroglia, which thus separates the three connectives. In preparations successfully fixed in either the corrosive sublimate or osmic acid mixtures, the cross section of the connectives shows nothing but the circular outlines of the cut nerve fibres, with their contents and a few neuroglia fibres penetrating the connective from the sides. The fibres vary greatly in size, from the large giant fibres, which are one

third the diameter of a lateral connective, to the smallest, which however are large enough to enable one to distinguish the circular outline of the sheath and its contents.

There are three giant fibres, one in each connective. Those in the lateral connectives are much larger than the median one.

On the median side of each of the paired connectives, close beneath the median connective, there is another very large fibre which, in some regions of the body, is but little smaller than the median giant fibre (Plate **5**, Fig. 31). These fibres, which I shall call set *A*, also stain very lightly, but they show no traces of a network.

The numerous fibres which constitute the remaining portions of the connectives stain more deeply. Most of them show no differentiation, but frequently the larger ones are more intensely stained in the centre than at the periphery.

In longitudinal sections of the connectives (Plate **3**, Fig. 26), the fibres appear as parallel bands separated by crinkled lines, — the fibre sheaths folded by a slight longitudinal contraction of the animal at the time of fixation. Many of the larger fibres, excepting set *A*, often show a darker central band corresponding to the darker centre of the transverse section. A few nuclei are scattered among the fibres of the connectives.

Transverse sections through the ganglia of the ventral chain present a single central filrous mass bordered ventrally and laterally by ganglionic cells. Bundles of neuroglia fibres pierce the central mass at intervals along the median plane, and divide the ganglion into symmetrical halves. The greater part of the fibrous mass consists of longitudinal fibres, but there are many fibres which traverse the ganglion in other directions.

The cells of the ventral ganglia do not vary as much in size, form, and structure as do those of the brain ; however, besides the uniformly granular ones of various sizes and shapes (Plate **2**, Figs. 13, 14, *A*), corresponding to those of class six in the brain, there are some cells (Fig. 14, *B*) which stain very lightly, and the cytoplasm of which is homogeneous with the exception of a few coarse granules of very limited distribution. There are only a few pairs of these cells in each ganglion ; one of the pairs belongs to the fibres of set *A*, and these are among the larger cells of the ganglion.

The coarse irregular granules of the cells last described occupy the middle of the cell, where they are arranged in the form of a hollow sphere, at the centre of which there is a round deeply staining granule (Fig. 14, *B*). This structure is undoubtedly what has been described as

a centrosome. It is not confined to this class of cells, but in good preparations occurs with such frequency that it may be said to exist in all the cells of the ventral cord (Fig. 13). The nucleus is always eccentric, and frequently, though not always, flattened. There are often two, three, or more centrosomes in a single cell. In one instance there were ten. In the cells whose cytoplasm is granular the centrosome does not appear as distinctly as it does in the others. However, when the staining has been successful, there appears at the centre of the cell a mass of granules which are larger and stain more deeply than those of the rest of the cell. The granules of this mass are arranged in the form of hollow spheres, the contents of which are destitute of all granules excepting the single round body at the centre.

6. Nerve Fibres.

a. Giant Fibres.

There are three giant fibres which traverse the ventral cord throughout its entire length (Plate **2**, Fig. 18, Plate **5**, Fig. 31); the pair of extremely large ones, which lie one on the outer side of each of the paired connectives, and the smaller unpaired one lying in the median connective. All these have the same peculiarities of structure. With the methods employed they stain very lightly and appear almost homogeneous. On close examination, however, the section of the fibre is seen to be made up of a small number of polygonal areas marked off by an indistinct network (Plate **1**, Fig. 3). This network apparently owes its existence simply to the presence of discrete masses of protoplasm, the boundaries of which give the appearance of a network. In longitudinal sections the giant fibres show the same structure, except that the polygonal areas are elongated in the direction of the axis of the fibre. When these fibres are stained in methylen blue, the stain is precipitated at the borders of the areas, producing a finely granular network in a homogeneous field of blue.

The paired fibres may be traced forward into the circum-œsophageal connectives to a point between the anterior cirrus ganglion and the commissural ganglion, where they divide into a number of small branches. The branches cannot be distinguished from other large fibres of the connective, but they appear to pass through the commissural ganglion to the optic ganglion. The fibres which connect the commissural and optic ganglia are processes of the cells of the optic ganglion, but since I was unable to trace a fibre continuously from the optic ganglion until it

united with the giant fibre, I cannot be sure that there is such a connection. I have found no other cells connected with these giant fibres.

The median giant fibre divides in the sub-œsophageal ganglion into several branches, which continue forward parallel with one another along the median plane. One of them I was able to trace to one of a group of large cells lying between the ventral ends of the circum-œsophageal connectives. The other cells of the group are connected with similar fibres, but I could trace only one continuously from the cell to the giant fibre.

The three giant fibres extend back into the last segment of the body without branching or changing their relative sizes or positions. Occasionally the median fibre in passing through a ganglion divides and allows the passage of a bundle of fibres between the two parts, which then immediately reunite, and the fibre continues on as before. This condition occurs frequently, but appears to be wholly accidental, since it is very irregular in the frequency of its occurrence, as well as in the size of the loop produced, and also in the relative sizes of the two divisions of the fibre. In one instance I found a similar condition in one of the lateral giant fibres, but it was not very well marked.

The giant fibres are pierced by many smaller ones, which pass directly through them (Plate **1**, Fig. 2). In the case of the lateral giant fibres this occurs most frequently near the places where the segmental nerves are given off from the ganglion. Sometimes the small fibres branch within the large one, the branches then continuing on through the giant fibre. In preparations stained with osmic acid, the small fibres stain much more deeply than the giant fibres, thus becoming very distinct. In a part of a methylen blue preparation which had not taken the stain, the small fibres traversing the giant fibres could be readily seen because they were more highly refractive than the giant fibre.

I cannot say that in successive segments the giant fibres are pierced by corresponding sets of smaller fibres, but there is at least one set which regularly traverses the giant fibre on passing out into the fourth (IV) and fifth (V) segmental nerves. This fibre will be described as set *B*.

b. Fibres of Set A.

Along the inner margin of the lateral connectives there lies a set of fibres (Plate **2**, Fig. 18, Plate **5**, Fig. 31) which in transverse section are almost as large as the median giant fibre, and resemble it in their resistance to stains. They differ from giant fibres, however, in the following particulars (compare Plate **4**, Fig. 27, *A*): — (1) They are arranged segmentally, one pair of fibres originating in each segment;

(2) Each fibre is connected with a single cell; (3) They do not extend through more than two segments; (4) They are not pierced by other fibres, nor (5) do they show the reticulum found in giant fibres; (6) They are branched. The cell (Plate **4**, Fig. 27) of which this fibre is a process lies on the ventral side of the ganglion near the origin of the third segmental nerve (III). The general direction of the process is forward, but at the outset it crosses and recrosses the median plane, decussating twice with its companion of the other side, one decussation being immediately behind and the other in front of the origin of the second (II) segmental nerve. After the second crossing the two fibres run side by side close beneath the median giant fibre, until they pass the first point of decussation of a similar set of fibres in the next anterior segment. Here they diverge and apparently break up into fibrillations or branches too small to be traced in preparations stained in the ordinary way. I have not succeeded in staining this fibre with methylen blue. This system is well developed in every segment from the last one of the tail to within twenty segments of the head, where the fibre gradually becomes smaller until, in the first three or four segments, it cannot be distinguished among the other fibres of the cord.

c. Fibres of Set B.

Next in size come the cells and fibres of set *B* (Plate **4**, Figs. 27, *B*, 28). The cells lie ventrally about midway between the origin of the first (I) and second (II) segmental nerves. From each cell a process extends forward and gradually rises into the middle of the ganglion. Opposite the origin of the fourth (IV) segmental nerve, the fibre turns squarely across the ganglion, running parallel to its mate, with which it decussates, and then divides into two branches, both of which go to the periphery; one through the fourth (IV), the other through the fifth (V) segmental nerve. The two fibres of a pair lie in contact for some distance where they cross from one side of the ganglion to the other (Plate **1**, Figs. 6, 7), and they anastomose at several points along the line of contact (Plate **4**, Fig. 28). The fibres of sets *A* and *B* are intimately associated at the point where they cross each other (Plate **1**, Fig. 6, Plate **3**, Figs. 22, 23), for they are not only in contact, but the smaller fibres lie in a deep indentation on the larger one. The relation of fibre *B* to the lateral giant fibre is still more intimate. Immediately after branching, one or both branches pass directly through the lateral giant fibre before passing out of the ganglion (Plate **1**, Fig. 2). Sometimes one branch may pass around the giant fibre, but still be in con-

tact with it, while the other branch passes directly through it. Sometimes the penetrating branch, instead of passing through the middle of the giant fibre, goes so far to one side that it does not become free from the sheath of the giant fibre, but is still wholly embedded in its substance.

d. Fibres of Set C.

The next fibre system (Plate **4**, Figs. 27, 30), set *C*, is apparently centripetal, since no cell was found connected with it, and since what appears to be the main fibre, entering the cord from the fourth segmental nerve (IV), immediately divides, forming the characteristic **Y** of centripetal fibres. One of the branches runs directly back and ends in fibrillations opposite the second nerve (II) of the succeeding segment. The other branch runs forward, and ends in a similar way opposite the second segmental nerve (II) of its own segment. Near its origin the second branch gives off a third which runs diagonally backward and across the ganglion, ending in a position symmetrical to the ending of the first branch. Since the counterpart of each of these three branches is found on the opposite side of the nerve cord, there must be six branches ending in each segment, on either side three, all of which are opposite the second segmental nerve (Fig. 27, II). The ends of the fibres are enlarged, and give off a few fibrillations. The three endings of each side of the body lie side by side, and are connected with one another by several ladder-like anastomoses (Plate **4**, Figs. 29, 30). The fibres of this set are rather large, and lie almost wholly on the ventral side of the cord. The third or decussating branches, however, are rather slender, and in crossing the ganglion first curve up and then down. Where the two fibres cross each other they are always in contact.

e. Peripheral Fibres.

The following are some of the fibres found in the parapodial ganglion (compare Plate **1**, Figs. 5, 8, Plate **5**, Fig. 39): (*a*) Fibres entering the ganglion from the second (II, Figs. 5, 39) segmental nerve pass through the ganglion and out either by the first (1) or by the fourth (4) parapodial nerves. (*b*) Fibres entering from the segmental nerve divide into two branches, one of which passes out through the second (2), the other through the third (3) parapodial nerve. Neither of these classes of fibres gives off fibrillations in the ganglion. (*c*) A third kind of fibre enters the parapodial ganglion from the segmental nerve, and ends in the ganglion in fibrillations.

The second (2) and third (3) parapodial nerves contain both motor and sensory fibres. In Figure 32 the motor fibres are shown, and in Figure 33 the sensory fibres of the third parapodial nerve. The motor fibres turn back along the muscles that move the setæ, and are lost among the muscle fibres. The cells of the sensory fibres lie far beneath the hypodermis. They send a process either to the hypodermis, or to the tissue around the openings through which the setæ project. At the latter place the fibres apparently end in fibrillations. Figure 37 represents a sensory cell of the anterior wall of the parapodium. The peripheral process of this cell enlarges just beneath the cuticula into a small knob, from which a fine prolongation extends out through the cuticula. Figure 38 represents a similar cell and nervous process in the posterior wall of the parapodium. In Figure 35 is seen a sensory cell from the base of the parapodium, and in Figure 36 one from the side of the body near the fourth segmental nerve.

Figure 34 shows the manner in which the motor fibres end in the longitudinal muscles, and Figure 40 shows the bushy endings of the fibres around the glands of the hypodermis between the bundles of circular muscles.

PART II. DISCUSSION.

1. Topography.

In methylen blue preparations it is usually not easy to determine the relation of the stained fibres to other organs, because of the difficulty of seeing structures which are not stained. For this reason I first made a study of the topography of the nervous system, tracing the nerves with considerable detail in preparations made by vom Rath's method. By this means nerves consisting of but a few fibres can be traced through serial sections. The account of the topography given in Part I. is more minute, but otherwise agrees in the main with that given by Quatrefages ('50) for Nereis. There is one important point, however, in which I cannot agree with Quatrefages. He states that the segmental nerve which he designates by the letter *o* (Planche 3) passes forward through the dissepiment to the preceding segment, thus making a nervous connection between two segments, in addition to that of the ventral nerve cord. From the diagram (Plate 1, Fig. 8) it will be seen that there is no segmental nerve passing from one segment to another in N. virens. The three nerves (I, IV, V) that arise near the intersegmental plane pass out parallel with that plane, two anterior to it and one

posterior. The segmentation of the longitudinal muscles is marked by an interdigitation of the fibres of one segment with those of the next. These interdigitations lie in the plane of the constriction of the body which gives the external appearance of segmentation. The line of attachment of the longitudinal muscles to the hypodermis (Plate **1**, Fig. 4) and the constriction in the protective tissue of the segmental ganglion (Plate **1**, Fig. 8) also lie in this plane, which, as will be seen from Figures 4 and 8, thus separates the fifth (V′) and first (I′) segmental nerves throughout their length. The segmental dissepiment is concave anteriorly. Its ventral median edge is attached in the constriction of the segmental ganglion, and is therefore in the intersegmental plane. But its lateral border is attached to the hypodermis, between the dorsal and ventral longitudinal muscles, anterior to the intersegmental plane and even anterior to the position of the fourth (IV′) segmental nerve in that region (Fig. 4). Hence, if the position of the dissepiment were taken to determine the boundary of segments, the fourth (IV′) and fifth (V′) segmental nerves would appear to pass backward from the segment in which they arise to the one succeeding it. But I have found no segmental nerve passing forward through the dissepiment as described by Quatrefages, nor indeed passing out of the segment in either direction, if we determine the boundary of segments by the segmentation of the musculature.

When compared with other annelids, we find that *Nereis presents a generalized condition with respect to its nervous system.* It indeed agrees very well with the description given by Lang ('88–'94) of the nervous system typical of Chætopods. In comparison with other Polychætes, however, Nereis shows a rather high degree of development, indicated by the deep position and elaborate protective tissue of the ventral nerve cord. In the majority of Polychætes the ventral nervous system lies embedded in the hypodermis, or intimately connected with it. In a few genera, however, such is not the case. Wawrzik ('92) shows that in Hermione and Aphrodite the ventral cord is entirely free from the hypodermis, and in this respect he classes these genera with the Oligochætes. Nereis would also belong to this class, since the ventral cord lies internal to the circular muscles, as it does in the Oligochætes.

2. Protective Tissue.

The nature and origin of the protective envelopes of the nervous system of Polychætes have been the subject of considerable discussion. The differences of opinion are probably due chiefly to real differences in

the animals studied. There is not much doubt, however, concerning the origin of the inner spongy layer, the neuroglia. Jourdan ('84) showed that the enveloping tissue of the central nervous system was intimately connected with the cells of the hypodermis. Rohde ('87) called this tissue "Subcuticularfasergewebe," and described it as a development of the basal processes of the cells of the hypodermis. Wawrzik ('92) made a comparison of a large number of Polychætes, and found that in all those in which the ventral cord was connected with the hypodermis the neuroglia was an integral part of the hypodermis cells. Haller ('89) denies the existence of the condition described by Rohde ('87) for Polynoë, since he found that the nerve cord was surrounded by a membrane which separated the neuroglia from the hypodermis. However it may be in this case, there certainly cannot be a connection between the hypodermis and neuroglia in such forms as Hermione, Aphrodite, and Nereis, in which these structures are clearly separated. But the condition found in so many other genera indicates that the neuroglia is derived from the ectoderm along with the nervous elements.

The neurilemma is apparently found only in those forms in which the nerve cord is free from the hypodermis. But even when present it may be so thin as to be readily overlooked. Such is sometimes the case at the posterior end of Nereis. On the other hand, it becomes very thick around the brain of Nereis, sometimes reaching a thickness of fully 100μ. Friedländer ('88) and Graber ('80) call this structure cuticular. Haller considers it simply the matted fibres of the neuroglia. Racowitza ('96) states that muscle fibres, as well as the neuroglia, contribute to make up the neurilemma. Where muscle fibres are attached to the outer surface of the neurilemma, or neuroglia fibres to its inner surface, membrane and fibre shade insensibly into each other, so as to suggest their structural identity. But, as has been shown above, as well as by other writers, the neurilemma in its reaction to stains is very different from either muscle or neuroglia. Whatever may be the weight of this evidence, it is clear that the neurilemma, the connective tissue of the muscles, and the tunica intima of the ventral longitudinal blood-vessel have the same structure, and must be derived from the same source. That source is most likely the mesoderm.

3. Brain.

Although the brain of Nereis gives rise to so many nerves, it is small and simple when compared with the brain, for example, of the

decapod Crustacea. In the latter, the fibrous part is relatively much greater, and the fibres are collected into small bundles forming numerous commissures between the various parts of the brain. Since the number and size of the nerves leaving the brain of decapod Crustacea is small compared with the size of the brain, the increase in the fibrous substance of the brain must be due to a greater development of the association fibres of all kinds, including not only fibres which lie wholly within the brain, but also those branches of centripetal and centrifugal fibres which bring the various parts of the brain into relation with one another. This condition is apparently correlated with the increased development of the "mushroom bodies" in Arthropods, as we shall see below.

4. "Mushroom Bodies."

The compact masses of small nuclei that lie in the anterior part of the brain of Nereis (Plate **3**, Figs. 24, 21) have been described by a number of writers, who have, however, usually expressed considerable doubt concerning their significance. Ehlers ('68) and Schröder ('86) describe this structure under the name "Nervenkörner." Rohde ('87) calls a similar structure in Polynoë and other Polychætes "Nervenkernen." Retzius ('95) refers to it as a "Haufen groben Körner," which he says are larger about the periphery of the mass. He thinks the larger granules may be cells, but doubts the cellular character of the smaller ones. His preparations were stained in methylen blue, but showed no processes connected with the nuclei. Haller ('89) discusses the nature of these structures at some length, and describes the elements as small multipolar ganglion cells. He calls the mass a "Tentakelganglion," and supposes it to be connected with the sense organs of the antennæ. Racowitza ('96) applies to it a similar term, "ganglion antennaire," but he does not mean to indicate thereby that the ganglion has any direct connection with the antenna. Haller objects to Rohde's application of the descriptive term "Hutpilz" to these ganglia "weil sie sehr leicht zu einer Verwechselung mit den hutpilzförmigen Körpern am Hirn der Insecten veranlassen dürfte, mit denen aber diese Ganglien nichts Homologes aufweisen können."

Notwithstanding this statement of Haller, I think there are good reasons for considering this organ as in some degree homologous with the mushroom bodies of the insect brain. The resemblance between the two appears more strongly, if we compare both with a corresponding structure in the brain of the crayfish. On the anterior lateral border of the brain of this Crustacean there is a triangular mass of small cells

which Krieger ('79) designates as gz_3. In my own preparations of the brain of the crayfish I find that this ganglion resembles the "ganglion antennaire" of Annelids in the following points. In both, (1) such ganglia are confined to the brain, no similar structure occurring in the ventral cord. (2) The ganglion is intimately associated with the masses of neuropil, which also occur nowhere but in the brain. (3) The small size of the nuclei and the meagre cytoplasm distinguish these cells from the other cells of the brain. (4) There is a peculiar arrangement of the cells in rows radiating from the neuropil. According to the description given by Kenyon ('96), the mushroom bodies of the honey bee exhibit the same peculiarities. The chief difference to be found in the three cases is the relative size of the nuclear and the neuropil masses, and in the arrangement of the two parts. In Nereis the nuclear mass partially surrounds the neuropil, whereas in the insect the relation of the two parts is reversed, the neuropil partly enveloping the nuclear mass. The crayfish presents an intermediate condition in this respect. The nuclear elements do not stain readily in methylen blue, — a condition also found by Allen and Bethe in Crustacea, and by Retzius in Nereis; but in the bee Kenyon obtained impregnations of the cells by the Golgi method. His preparations show that the cells of these ganglia send processes into the neuroglia, where they end in dendrites almost as complex as those found in the brain of Vertebrates. Since in the worm there is relatively little neuropil, the dendrites of the associated cells will probably be found to be less well developed. Kenyon's supposition that the intelligence of the insect is to be accounted for by the complexity of the relations between the nervous elements made possible by these association fibres seems quite plausible; and if we apply the same argument to the worm, we may suppose its low intelligence to be in part correlated with the small amount of neuropil, or, in other words, the limited development of the association fibres.

Aside from the cells of this ganglion and those connected with the ciliated groove, the brain of Nereis contains about as many cells as a typical ganglion of the ventral chain. If we compare the brain with the ganglia of the ventral chain, or if we compare the central nervous system of Annelids with that of Arthropods, the only structural condition to be found which warrants the supposition that it is correlated with the supposed psychic functions of the brain is the mushroom body and the related development of association fibres. This correlation has often been pointed out for insects, and I think we may extend the observation to decapod Crustacea and Annelids.

Racowitza shows that those Polychætes which lack antennæ also lack the "ganglion antennaire." He does not prove, however, that the cells of this ganglion may not be present in the brain, and therefore does not exclude the possibility that the ganglion may be present in a diffuse form.

5. Optic Ganglion.

The condition of the optic ganglion in Nereis virens is of interest, because it serves to explain what have hitherto appeared to be unaccountable differences between several species of Nereis. Carrière ('85, pp. 33–35) described this ganglion for N. cultrifera, and Retzius ('95) found it in N. diversicolor. On the other hand, Carrière says there is no such ganglion in a species from Norderney which he examined, and Graber ('80) and Haller ('89) also failed to find it in Nereis costæ. It seemed strange that a central ganglion, like this, should exhibit such will-of-the-wisp peculiarities in passing from one species to another so closely related to it. I think, however, that the condition of this ganglion in N. virens shows clearly what becomes of the ganglion when it disappears from its place beneath the anterior eye, as in N. costæ. In N. virens the ganglion evidently lies partly beneath the eye and partly within the brain capsule. A few scattering cells show the path the ganglion has taken in its migration inward or outward. It is not only the great similarity in the appearance of the cells and the contiguity of the two parts that makes this view seem probable, but also the cells of both groups send their processes to the commissural ganglion and neither part appears to be directly connected with the brain. It is not apparent what is the relation of the ganglion to the anterior eye. Carrière thought the ganglion formed part of the connection between the eye and the brain, but this cannot be, for later writers agree that the anterior eye as well as the posterior is innervated directly from the brain.

The posterior end of the brain deserves more careful study than I have as yet been able to give it; I shall therefore simply call attention to a few facts. Five of the six kinds of cells described for the brain are to be found in the posterior part, and of these five three are not found elsewhere. Moreover these three are the most peculiar ones, — those of the second, third, and fourth classes. This portion of the brain is partly separated from the remainder of it, and is intimately connected with the surface at the ciliated grooves and at the dorsal sensory regions through the thirteenth (XIII) and fourteenth (XIV) nerves. Perhaps

the whole is to be considered a complex sensory organ, analogous to the olfactory organ of Vertebrates in its intimate relation with the brain. Retzius shows that the sensory fibres of the ciliated groove are processes from bipolar cells of this region. The fibres of the fourteenth pair of nerves are the processes of cells similar in form and position to the bipolar cells of the thirteenth nerve.

6. Ventral Nerve Cord.

The structure of the ventral nerve cord has been well described for Lumbricus by Friedländer ('94), and Hatschek ('89–'91) has given a good figure of a transverse section of the ventral cord of Sigalion. Most writers, however, have not succeeded in preparing the ventral cord so as to show clearly that the connectives consist wholly of longitudinal fibres. There is nowhere in the ventral cord a neuropil in the sense of that which is found in the brain. There are small masses of fibrillations in the ganglia, of course, but they simply fill up the interstices between the fibres, and never occur in masses large enough to produce the punctate appearance peculiar to the neuropil of the brain.

The paucity of nuclei among the fibres of the cord will not permit one to regard the fibre sheaths as composed of the expansions of non-nervous cells. In the decapod Crustacea the fibre sheaths are nucleate, and in the case of the sheath of giant fibres the nuclei are so numerous that the sheath may be described as a flat endothelium. In Nereis, however, the sheath must be a product of the fibre itself.

7. Centrosomes.

Since Lenhossék ('95) announced the discovery of the centrosome in the adult nerve cells of the frog, there have appeared a number of papers describing similar structures in Reptiles (Buehler, '95), Cyclostomes (Schaffer, '96), Molluscs (McClure, '96), and Worms (Lewis, '96). Heidenhain ('97) summarizes the evidence and gives a bibliography. Dahlgren ('97) describes what he calls a centrosome artifact in the spinal ganglia of the dog. This artifact, he says, is produced by the formation of a crystal of corrosive sublimate in the cell. In Nereis I find the best demonstrations of centrosomes in preparations that have been fixed in corrosive sublimate, but they also occur in preparations fixed in the osmic acid mixture of vom Rath. I think there is no reason for considering the phenomenon an artifact in this case. I will simply call attention in this connection to two facts that were mentioned previously;

first, the general occurrence of the centrosome in the cells of the ventral ganglia, and, secondly, the large number of centrosomes that may occur in a single cell. I have no explanation to offer for the latter condition. Since the structures appear only under special conditions of staining, and since I had only one preparation of the brain stained in iron-hæmatoxylin, I am not in a position to say whether the centrosome occurs in the brain or not, even though I failed to find it in the preparations I had at hand.

8. Nerve Fibres.

a. Giant Fibres.

The literature concerning giant fibres is voluminous, and extensive bibliographies on the subject may be found in the works of Eisig ('87) and Friedländer ('88, '94). I shall concern myself here with only a few of the many points in which these fibres have given rise to discussion. It has been frequently demonstrated that they are the processes of cells, and they have been taken by many writers to be nervous in function, but some authors still doubt that that is their nature; Lenhossék ('92), for example, has recently expressed the conviction that they are not. The most serious objection that has been urged against their nervous nature is the absence of evidence that they are related to other nervous structures, either by fibrillations within the cord or by centrifugal branches.

I think there is sufficient reason for maintaining that in Nereis virens the fibres of set *B* serve as branches for the lateral giant fibres. I therefore believe that the function of the latter is to transmit nervous impulses like ordinary nerve fibres.

The most peculiar feature of giant fibres is that they are often connected with more than one cell. In 1881, Spengel ('81) arrived at the conclusion that in Halla there was a fusion of giant fibres, but he had no direct evidence. Rohde ('87), however, shows conclusively that at least one giant fibre in the ventral cord of Sthenelais is formed by the union of the processes of two cells. These lie in the brain and send their processes through the circum-œsophageal connectives to the sub-œsophageal ganglion, where they fuse and whence they continue as a single fibre throughout the entire length of the animal. Friedländer ('88) found that the lateral giant fibres of the earthworm are connected with a number of cells in the posterior segments of the animal. This discovery was confirmed by Cerfontaine ('92), who also found that the median fibre is connected with several cells at the anterior end of the

body. In Rhynchelmis, too, according to Vejdovsky ('88, '92), the giant fibres are connected with a number of cells and in such a way that each might well be considered a bundle of fibres. Finally, Lewis ('96) describes in a Moldanid a giant fibre which is connected with a large number of cells. There is not yet sufficient evidence to show whether the giant fibres of Chætopods are more frequently multicellular or unicellular, but there can be no doubt that they are often multicellular.

The giant fibres of Crustacea have not been so well investigated as those of Chætopoda, but in Homarus, at least, each giant fibre is the process of a single large cell, according to the description of Allen ('94).

Our present knowledge of the giant fibres (in the sense in which I use the term) might be summarized in the following way. The giant fibres of Annelids and Crustacea are much larger than ordinary fibres, and extend for long distances through the central nerve cord; they are connected either with one very large cell or with the processes of several cells, and they give off neither fibrillations nor branches. In some cases, as in Lumbricus, there are anastomosing bars, or connections, between two giant fibres; in others, the giant fibres may divide or they may fuse with one another, but in no case is there an ending corresponding to the fibrillations of other nerve fibres by which the giant fibres might be put in connection with other nervous structures. In Nereis, however, there is a very intimate connection between the lateral giant fibres and the centrifugal branches of set *B*, as I have shown, and by this system of connections the giant fibres are put in relation with every segment of the body.

What the function of such giant fibres may be is readily conceivable, and I believe the true explanation has already been offered by several writers. Vignal ('83) suggested that their purpose was to bring about a more direct connection of the nervous system as a whole than is done by less extensive fibres. Friedländer's experiments on the earthworm show that, when the ventral cord is severed, the sudden longitudinal contraction of the body can no longer be brought about. Friedländer argues that, since these fibres are the only ones, so far as we know, that pass through the entire length of the animal, it is reasonable to suppose they are the ones that conduct the stimulus for this contraction.

In Nereis I have frequently noted a sudden longitudinal contraction where there was apparently no stimulus except the passing of a shadow. I have not yet had the opportunity to test this further, to determine if the stimulus proceeded from the eyes, but I found that no tactile stimulus was sufficient to produce such a sudden and general longitudinal

contraction. When the habits of the animal are considered, it is possible to understand what the function of such a contraction brought about by the stimulus of light might be. The worm lives in the mud in burrows, and frequently rests with the anterior end above the surface, while the remainder of the body is in the burrow. Under such circumstances the longitudinal contraction would cause the animal to retreat into the burrow, for longitudinal contractions are in general accompanied by the pointing of all the parapodia towards that end of the body from which the stimulus comes. For example, if the stimulus is applied at the anterior end, the parapodia are all thrown forward, and the longitudinal contraction of the body immediately follows. This will cause the anterior end to move towards the tail while the latter remains stationary, since the position of the parapodia prevents movement of the body in the opposite direction. Now, if the shadow cast by a predatory animal were to bring about this movement, the mechanism would be of vital importance to the worm. Perhaps the importance of the function and the great extent of the movement brought about help to account for the large development of the giant fibres. The objection may be urged that since the phenomena which I have described for Nereis have not been found elsewhere, they cannot be of general importance, even if the condition be admitted for Nereis. But the exceptional conditions under which such phenomena can be observed render it probable that they may have been overlooked even when present.

It must be remembered that, in order to demonstrate the passage of one fibre through another, there must be a differential staining of the substance of the two fibres. Only in preparations fixed and stained by the method of vom Rath, and not in all of these, have I obtained such a differentiation. Successful preparations, however, leave no doubt concerning the actual relation of the fibres, for I have carefully compared series of sections cut in each of the three cardinal planes, and always with the same result.

If, then, the giant fibres are nervous in function, the neuron theory of Waldeyer ('91) will require considerable modification. The nervous element is not always unicellular, but may consist of a number of cells united in function. The nervous connection between fibres is not always through fibrillations; it may be directly between the axis cylinders themselves.

b. Fibres of Set A.

Since little is known about the relations of the fibres of set *A* to other fibres, we cannot say much about their probable function. Nevertheless,

there are several facts which point to a connection with the forward locomotion of the animal. The worm advances by a rhythmical movement of the parapodia, which begins at the posterior end and passes toward the head. With this movement there is usually associated a serpentine motion of the body, which also passes from behind forward. Both movements are less vigorous near the head, and the serpentine disappears entirely between the twentieth and tenth segments. The size of the fibres of set *A* in a given region corresponds to the degree of activity of the locomotor movements of that region. Whether this fact is more than a mere coincidence I cannot say, but it would seem to be so. Besides, if there is a causal relation between the condition of these fibres and the locomotor movements, we may even account for the enormous size of the fibres on the ground of their functional importance. Another evidence of this correlation is the serial arrangement of the fibres, which may be connected with the progressive character of the motor excitation, and with the postero-anterior disposition of each fibre, the latter corresponding to the direction of the movement.

Although these speculations concerning the function of giant fibres are purely tentative, they may serve as a basis for physiological experiments.

c. Fibres of Set B.

In describing the fibres of set *B* (Plate **4**, Figs. 27, 28) I merely mentioned the fact of an anastomosis between the axis cylinders of the components of each pair. I wish here to discuss the subject more fully. The description of these fibres was by no means based wholly on methylen-blue preparations. Indeed, all the facts, excepting that of anastomosis, were demonstrated on serial sections before an impregnation by methylen-blue was obtained. The fibres are so large that they can easily be traced through serial sections. This fact is important in considering the value of the evidence for anastomosis.

I have carefully examined seventeen pairs of these in serial sections cut in one or the other of the three cardinal planes of the body, and in addition eight pairs stained in methylen-blue and examined before cutting. Where the fibres of a pair crossed the ganglion they were always in contact with each other, and, with one exception, they ran parallel for a considerable distance. In the exceptional case the fibres crossed each other at an angle of about ten degrees, which still allowed a line of contact equal in length to one fourth the width of the ganglion. The fibres usually cross the ganglion at right angles to its longitudinal axis, but in one instance they crossed at an angle of about sixty degrees (Plate **1**,

Fig. 7). Thus, one of the fibres partially retraces its course in order to maintain a course parallel with its fellow. Sagittal sections (Plate **3**, Figs. 22, 23) show that the fibres are always flattened on their apposed faces. That part of the sheaths which forms the dividing wall is usually very thin, and in some cases seems to be wholly wanting. In the preparations which are best preserved, however, the dividing wall can always be seen. I have not been able to demonstrate satisfactorily anastomoses in preparations made by the more usual histological methods. In methylen-blue preparations the fibres do not appear to be in contact, but this is due to a shrinking of the axis cylinder within the sheath produced during the fixing of the stain. The anastomoses, however, do exist, and are clearly shown in methylen-blue preparations (Plate **4**, Fig. 28); they proceed from small elevations on the opposed faces of the fibres. From what has gone before, it is evident that the anastomosing bars simply pierce the thin membrane that separates the two fibres, and that they practically lie wholly within the fibre sheaths. Hence they cannot be regarded as fibrillations fused by the action of the methylen-blue. The fibrillæ of the axis cylinder pass out into the anastomosing bars, but whether they pass completely across from one fibre to the other I cannot say. There is, however, a distinct interdigitation of the fibrillæ of the opposite fibres. The appearance of the preparations gives one the impression that there has been a breaking of the fibrillæ of the anastomoses due to the shrinking of the fibres. The anastomoses are not always as evident as they are in the case reproduced in Figure 28, but there is always some indication of them. This may consist simply of the pointed elevations arranged in pairs opposite each other on the fibres.

Since the cells of set *B* are situated in a central organ, they are probably motor, and since the fibres are united in bilaterally symmetrical pairs, they probably act in concert. Such animals as Annelids differ from more complex organisms in that many of their movements are in unison on the two sides of the body. The longitudinal contractions and expansions of the body are examples. In Nereis the movement of all the parapodia backward or forward, when the animal is touched at one end or the other, is another instance. When such movements are so frequent and of such vital importance, one may well expect to find an intimate association of the related nerve fibres.

Allen ('96) describes decussating nerve elements in the abdominal ganglia of the lobster so closely united that he was unable to resolve them into their constituent parts. He finds, however, that similar elements in the thorax are not so intimately related. At another place he

makes the statement that these elements of the abdomen innervate the abdominal muscles, while those of the thorax go to the ambulatory appendages. The reason for the difference in the arrangement of the nerve elements will be immediately perceived. The muscles of the abdomen act bilaterally in unison, hence the union of the associated nerve elements. In the case of the ambulatory appendages there is little movement in unison, hence the corresponding independence of the fibres concerned.

d. Fibres of Set C.

Lenhossék ('92) makes the general statement relative to the sensory fibres of the earthworm, that they do not cross the ventral nerve cord, but end in fibrillations on the side from which they enter the cord. The fibre *C* of Nereis is an interesting exception to this rule. Concerning the anastomoses of this system I need say but little. The fibres are so large, the anastomoses so numerous and distinct, and the fibre in such excellent condition for study, that there is small chance for error. There is no vacuolation of the fibre nor other evidence to lead one to conclude that there has been a fusion of fibrillations in the manner suggested by Cajal ('96). I have seen no evidence of anastomosis between fibres except those of set *B* and set *C*, and here the anastomosis is always between fibres of the same set.

I wish to call attention to one more point relative to these fibres. The small decussating branches cross the ganglion by a sinuous course, and yet where they cross each other they are invariably in contact. Why this should be so is difficult to say, unless the function of the fibres necessitates such contact. A similar relationship is also to be found between fibres of other sets, as in the case of the fibres of sets *A* and *B*, as described above. Although physiologists do not recognize contact between axis cylinders as a means of bringing fibres into functional relation, it seems to me quite probable that such a relation exists in some cases.

Summary.

1. The central nervous system of Nereis virens occupies a deeper position than does that of most Polychætes. It is separated from the hypodermis by the circular muscles, and is enveloped by an elaborate protective tissue.

2. The protective tissue consists of two parts; an inner spongy layer, the neuroglia, of ectodermic origin, and an outer sheath, the neurilemma, of mesodermic origin.

3. The "mushroom bodies" of insects and decapod Crustacea are represented in the brain of Nereis by the anterior masses of small nuclei.

4. The optic ganglion, which in some species of Nereis lies beneath the anterior eye, may in other species lie within the brain capsule.

5. There is no neuropil in the ventral nerve cord.

6. There are three longitudinal connectives between each two successive ganglia of the ventral nerve cord, one small median and two larger lateral ones.

7. The sheaths of the nerve fibres of the ventral cord have no nuclei, and hence must be a product of the fibres themselves.

8. The nerve cells of the ventral cord commonly have one or more centrosomes.

9. The giant fibres are nervous in function, and are put into relation with peripheral organs through ordinary centrifugal fibres.

10. The giant fibres give off no fibrillations, and nervous relation with other fibres is established directly between the axis cylinders.

11. Certain decussating fibres are always united in pairs by anastomoses between the axis cylinders where they cross each other.

12. Certain centripetal fibres of the same set are always united by anastomoses between the ends of the branches.

13. Contact between axis cylinders may possibly be one of the means of bringing nerve fibres into functional relation with each other.

In conclusion, I wish to acknowledge my indebtedness to Professor E. L. Mark for kindly advice and assistance rendered me in many ways while pursuing my studies in the Zöological Laboratory of Harvard University. I gladly avail myself of this opportunity to express to him my sincere thanks.

BIBLIOGRAPHY.

Allen, E. J.
'94. Studies on the Nervous System of Crustacea. Quart. Jour. Micr. Sci., Vol. 36, N. S., pp. 461–498, Pls. 35–38.

Allen, E. J.
'96. Studies on the Nervous System of Crustacea. Quart. Jour. Micr. Sci., Vol. 39, N. S., pp. 33–50, Pl. 4.

Bethe, A.
'95. Studien über das Centralnervensystem von Carcinus Maenas, nebst Angaben über ein neues Verfahren der Methylenblaufixation. Arch. f. mikr. Anat., Bd. 44, Heft 4, pp. 579–622, Taf. 34–36.

Buehler, A.
'95. Protoplasma-Structur in Vorderhirnzellen der Eidechse. Verhandl. phys.-med. Gesellsch. zu Würzburg, N. F., Bd. 29, No. 6, pp. 209–252, Taf. 3–5.
Also separate, 44 pp., 3 Taf., 1895.

Cajal, Ramon y.
'96. Nouvelles contributions à l'étude histologique de la rétine et à la question des anastomoses des prolongements protoplasmiques. Jour. Anat. et Physiol., Tome 32, No. 5, pp. 481–543, Pls. 12–15.

Carrière, J.
'85. Die Sehorgane der Thiere vergleichend-anatomisch dargestellt. München und Leipzig. vi + 205 pp., 147 Abbildg.

Cerfontaine, P.
'92. Contribution à l'étude du système nerveux central du Lombric terrestre. Bull. Acad. roy. Belgique, Série 3, Tome 23, pp. 742–752, Pls. 1, 2.

Dahlgren, U.
'97. A Centrosome Artifact in the Spinal Ganglion of the Frog. Anat. Anzeiger, Bd. 13, No. 4, 5, pp. 149–151, 2 Figs.

Ehlers, E.
'64–68. Die Borstenwürmer (Annelida chætopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Leipzig, Engelmann, xx + 748 pp., 24 Taf.

Eisig, H.
'87. Monographie der Capitelliden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte nebst Untersuchungen zur vergleichenden Anatomie und Physiologie. Fauna u. Flora des Golfes von Neapel. Monographie XVI., Berlin, xxvi + 906 pp., 37 Taf.

Friedländer, B.
'88. Beiträge zur Kenntnis des Centralnervensystems von Lumbricus. Zeit. f. wiss. Zool., Bd. 47, Heft 1, pp. 47–84, Taf. 9, 10.

Friedländer, B.
'89. Ueber die markhaltigen Nervenfasern und Neurochorde der Crustaceen und Anneliden. Mitth. Zool. Stat. Neapel, Bd. 9, Heft 2, pp. 205–265, Taf. 8.

Friedländer, B.
'94. Altes und Neues zur Histologie des Bauchstranges des Regenwurms Zeit. f. wiss. Zool., Bd. 58, Heft 4, pp. 661–693, Taf. 40.

Friedländer, B.
'95. Ueber die Regeneration herausgeschnittener Theile des Centralnervensystems von Regenwürmern. Zeit. f. wiss. Zool., Bd. 60, Heft 2, pp. 249–283, Taf. 13, 14.

Graber, V.
'79. Morphologische Untersuchungen über die Augen der freilebenden marinen Borstenwürmer. Arch. f. mikr. Anat., Bd. 17, pp. 243–323, Taf. 18–20.

Haller, B.
'89. Beiträge zur Kenntniss der Textur des Central-Nervensystems höherer Würmer. Arbeit. Zool. Inst. Wien, Tome 8, Heft 2, pp. 175–312, Taf. 16–20.

Hatschek, B.
'89–'91. Lehrbuch der Zoologie, u. s. w. Lieferungen 1–3. Jena, G. Fischer. 432 pp. [unfinished].

Heidenhain, M.
'97. Ueber die Mikrocentren mehrkerniger Riesenzellen, sowie über die Centralkörperfrage im Allgemeinen. Morphol. Arbeiten [Schwalbe], Bd. 7, Heft 1, pp. 225–280.

Jourdan, E.
'84. Le cerveau de l'Eunice Harassii et ces rapports avec l'hypoderme. Comptes Rendus Acad. Sci. Paris, Tome 98, pp. 1292–1294.

Kenyon, F. C.
'96. The Brain of the Bee. Jour. Comp. Neurology, Vol. 6, No. 3, pp. 133–210, Pls. 14–22.

Krieger, K. R.
'80. Ueber das Centralnervensystem des Flusskrebses. Zeit. f. wiss. Zool., Bd. 33, Heft 4, pp. 527–594, Taf. 31–33.

Lang, A.
'88–'94. Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere. Jena, G. Fischer, 1888–94, xvi + 1198 pp., 251 Abbildg.

Lenhossék, M. von.
'92. Ursprung, Verlauf und Endigung der sensibeln Nervenfasern bei Lumbricus. Arch. f. mikr. Anat., Bd. 39, Heft 1, pp. 102–136, Taf. 5.

Lenhossék, M. von.
'95. Centrosom und Sphäre in den Spinalganglienzellen des Frosches. Sitzb. phys.-med. Gesellsch. Würzburg, Jahr. 1895, No. 5–7, pp. 79–103.

Lenhossék, M. von.
'95a. Centrosom und Sphäre in den Spinalganglienzellen des Frosches. Arch. f. mikr. Anat., Bd. 46, Heft 2, pp. 345–369, Taf. 16, 17.

Lewis, M.
'96. Centrosome and Sphere in Certain of the Nerve Cells of an Invertebrate. Anat. Anzeiger, Bd. 12, No. 12, 13, pp. 291–299, 11 Figs. Sept. 2.

McClure, C. F. W.
'96. On the Presence of Centrosomes and Attraction Spheres in the Ganglion Cells of Helix Pomatia, with Remarks upon the Structure of the Cell Body. Princeton Coll. Bull., Vol. 8, No. 2, pp. 38–41.

Quatrefages, A. de.
'50. Études sur les types inférieures de l'embranchement des Annelés. Ann. Sci. Nat., Série 3, Zool., Tome 14, pp. 281–289.

Racowitza, E. G.
'95. Sur le rôle des Amibocytes chez les Annélides polychètes. Comptes Rendus Acad. Sci. Paris, Tome 120, No. 8, pp. 464–467.

Racowitza, E. G.
'96. Le lobe céphalique et l'encéphale des annélides polychètes. (Anatomie, morphologie, histologie.) Arch. Zool. Exp., Série 3, Tome 4, No. 1, 2, pp. 133–343, Pls. 1–5.

Rath, O. vom.
'95. Zur Conservirungstechnik. Anat. Anzeiger, Bd. 11, No. 9, pp. 280–288.

Retzius, G.
'91. Zur Kenntniss des centralen Nervensystems der Würmer. Biol. Unters., N. F., Bd. 2, pp. 1–28, Taf. 1–10.

Retzius, G.
'95. Zur Kenntniss des Gehirnganglions und des sensiblen Nervensystems der Polychäten. Biol. Unters., N. F., Bd. 7, pp. 6–11, Taf. 2, 3.

Rohde, E.
'87. Histologische Untersuchungen über das Nervensystem der Polychäten. Zool. Beiträge [Schneider], Bd. 2, Heft 1, pp. 1–81, Taf. 1–7.

Sars, M.

'35. Beskrivelser og iagttagelser over nogle mœrklige eller nye i Havet ved den Bergenske Kyst lebende Dyr, af Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes Classer, etc. Bergen. 81 pp., 15 pls.

Schaffer, J.

'96. Ueber einen neuen Befund von Centrosomen in Ganglien- und Knorpelzellen. Sitzb. Akad. Wissensch. Wien, math.-naturw. Cl., Bd. 105, Heft 2, Abth. 3, pp. 21–28, 1 Taf.

Schröder, G.

'86. Anatomisch-histologische Untersuchung von Nereis diversicolor, O. Fr. Müll. Inaug.-Dissertation. Rathenow. Carl Köppel. 43 pp., 1 Taf.

Spengel, J. W.

'81. Oligognathus Bonelliæ, eine schmarotzende Eunice. Mitth. Zool. Stat. Neapel, Bd. 3, Heft 1 u. 2, pp. 15-52, Taf. 2–4.

Vejdovsky, F.

'88–'92. Entwicklungsgeschichtliche Untersuchungen. Prag, iv + 401 pp., u. Atlas mit 32 Taf.

Vignal, W.

'83. Recherches histologiques sur les centres nerveux de quelques invertébrés. Arch. Zool. Exp., Série 2, Tome 1, No. 2, pp. 267–412, Pls. 15–18.

Vom Rath, O. *See* **Rath, O. vom.**

Waldeyer, W.

'91. Ueber einige neuere Forschungen im Gebiete der Anatomie des Centralnervensystems. Deutsch. med. Wochenschrift, Jahrg. 1891, No. 44.
Also separate. G. Thieme, Leipzig, 1891, 64 pp., 10 Figs.

Wawrzik, E.

'92. Ueber das Stützgewebe des Nervensystems der Chaetopoden. Zool. Beiträge [Schneider], Bd. 3, Heft 2, pp. 107–127, Taf. 14–19.

EXPLANATION OF PLATES.

All Figures, except 1, 5, 8, 27, and 39, were outlined with the camera lucida. Figures 28–30 and 32–41 were drawn from methylen-blue preparations.

ABBREVIATIONS.

a.	Anterior.	*gn. sg.*	Segmental ganglion.
anastm.	Anastomosis.	*h'drm.*	Hypodermis.
ax. cyl.	Axis cylinder.	*mu.*	Muscle fibres.
ceb.	Brain.	*mu. crc.*	Circular muscles.
cir.	Cirrus.	*mu. lg.*	Longitudinal muscles.
cir. ta.	Tentacular cirrus.	*mu. ob.*	Oblique muscles.
cl. cil.	Ciliated cell.	*n.*	Nerve.
cl. sns.	Sensory cell.	*n'cd.*	Giant fibre.
coms. crc-œ.	Circum-œsophageal commissure.	*n'gli.*	Neuroglia.
		nl.	Nucleus.
con't. lg. l.	Lateral longitudinal connective.	*n'lem.*	Neurilemma.
		n'pil.	Neuropil.
con't. lg. m.	Median longitudinal connective.	*n. pa-coms.*	Para-commissural nerve.
		oc.	Eye.
c'so.	Centrosome.	*p.*	Posterior.
cta.	Cuticula.	*po. sg.*	Pore of segmental organ.
di'sep.	Dissepiment.	*rtl.*	Reticulum.
fbr.	Fibrillations.	*sg. ce.*	Cephalic segment.
fbr. mot.	Motor fibres.	*set.*	Seta.
fbr. n.	Nerve fibres.	*sul. cil.*	Ciliated groove.
gn. coms.	Commissural ganglion.	*tu. fbr.*	Fibre sheath.
gn. pa'pd.	Parapodial ganglion.	*tu. i.*	Tunica intima.
gn. sb-œ.	Sub-œsophageal ganglion.	*va. sng.*	Blood-vessel.

PLATE 1.

Fig. 1. Diagram showing the disposition of the nerves of the brain and sub-œsophageal ganglion in dorsal aspect. In order to show the commissural ganglion and its nerves, the right anterior eye has not been indicated; I, V, α, β, γ, nerves to the proboscis; II, nerve to the antenna; III, IV, VII, δ, ϵ, ζ, η, nerves to the muscles and the general surface of the head; θ, commissure between the anterior and posterior cirrus ganglia; VI, nerve to the palp; VIII, IX, X, nerves from the brain to the commissural ganglion; XI, XII, optic nerves; XIII, nerve of the ciliated groove; XIV, three openings in the dorsal surface of the brain capsule, through which loose bundles of nerve fibres pass to the integument of the mid-dorsal region of the cephalic lobe.

Fig. 2. Para-sagittal section of a giant fibre to show the passage through it of a fibre of set *B* (compare Fig. 27). In this case the branching of the fibre *B* takes place within the giant fibre, and the axis cylinder of fibre *B* is shrunken.

Fig. 3. Cross section of a lateral giant fibre, to show the reticulum.

Fig. 4. Frontal section of the body wall between two parapodia, to show the relative positions of nerves IV′, V′, and I′, and of the attachment of the longitudinal muscles and the dissepiment.

Fig. 5. Diagram of posterior aspect of part of a cross section, showing the disposition of the parapodial nerves. The second and third parapodial nerves (compare Fig. 8) are designated by 2 and 3 respectively.

Fig. 6. Frontal section of a segmental ganglion, showing the intimate relation between the fibres of sets *A* and *B* (compare Fig. 27).

Fig. 7. Section similar to that in Fig. 6 showing the relation of the decussating parts of fibres *B*; also showing exceptional oblique course across the ganglion.

Fig. 8. Diagram showing the disposition of the segmental and parapodial nerves of a typical segment. I, II, III, IV, V, the five segmental nerves numbered from in front backward. 1, 2, 3, 4, the four parapodial nerves.

HAMAKER-NERVOUS SYST. NEREIS.

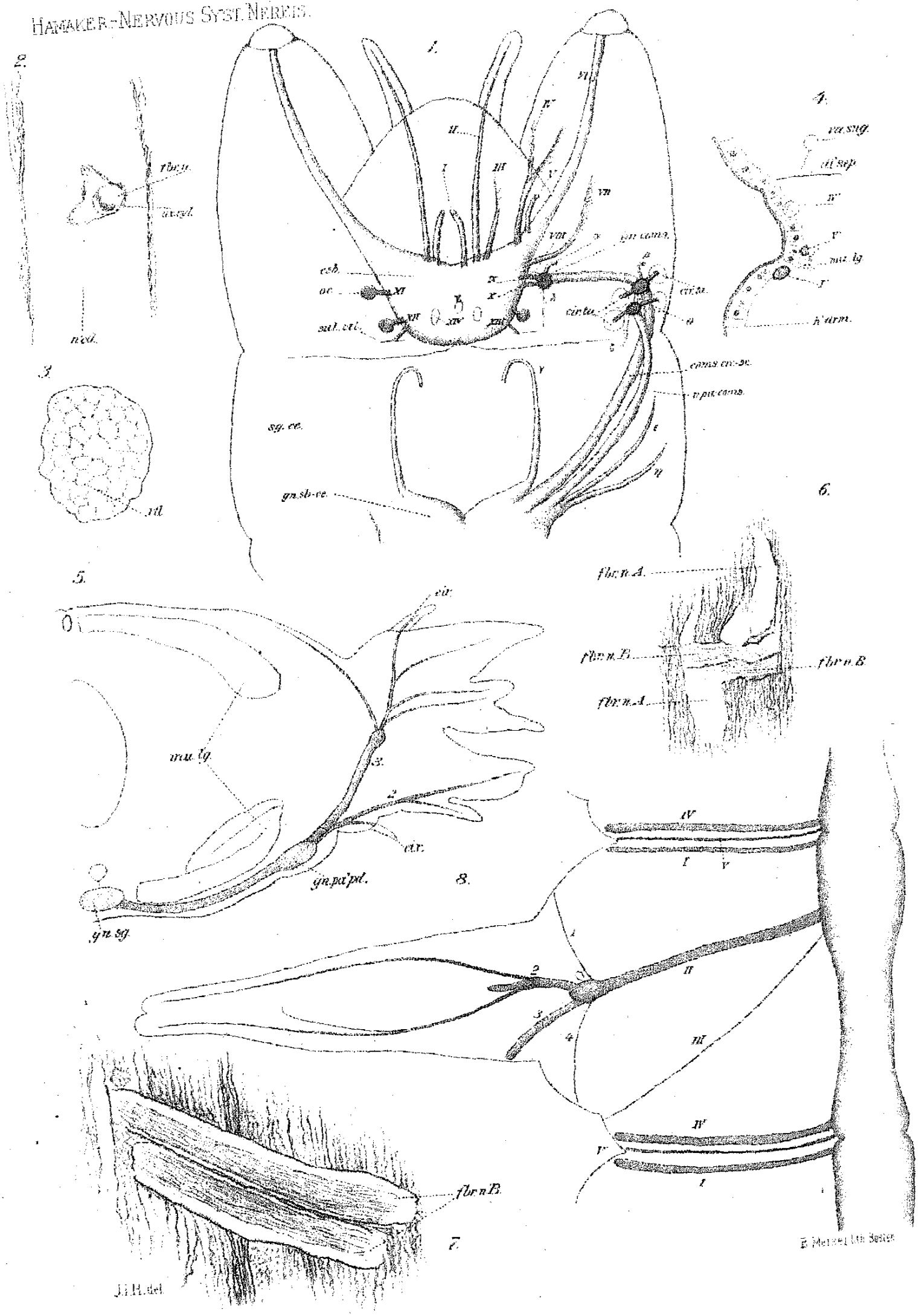

PLATE 2.

Fig. 9. Transverse section through the posterior end of the brain.
Fig. 10. Pigment (?) from the posterior part of the brain.
Figs. 11 and 12. Nerve cells of the fourth and third classes of the brain respectively.
Fig. 13. A group of four ganglionic cells of a segmental ganglion, in frontal section, to show centrosomes.
Fig. 14. *A*, ordinary ganglionic cell. *B*, one of the large cells of set *B* (compare Fig. 27). The cytoplasm is not granular and takes little stain, excepting the large irregular granules around the centrosomes.
Fig. 15. Brain nerve cell of the second class.
Figs. 16 and 17. Brain nerve cells of the sixth class.
Fig. 18. Transverse section through the posterior end of a segmental ganglion from the region of the fifteenth segment. It shows the connection between the neurilemma and the tunica intima of the ventral blood-vessel; also the position of the ventral nerve cord relative to the hypodermis and the circular muscles.
Fig. 19. Brain nerve cell of the fifth class.

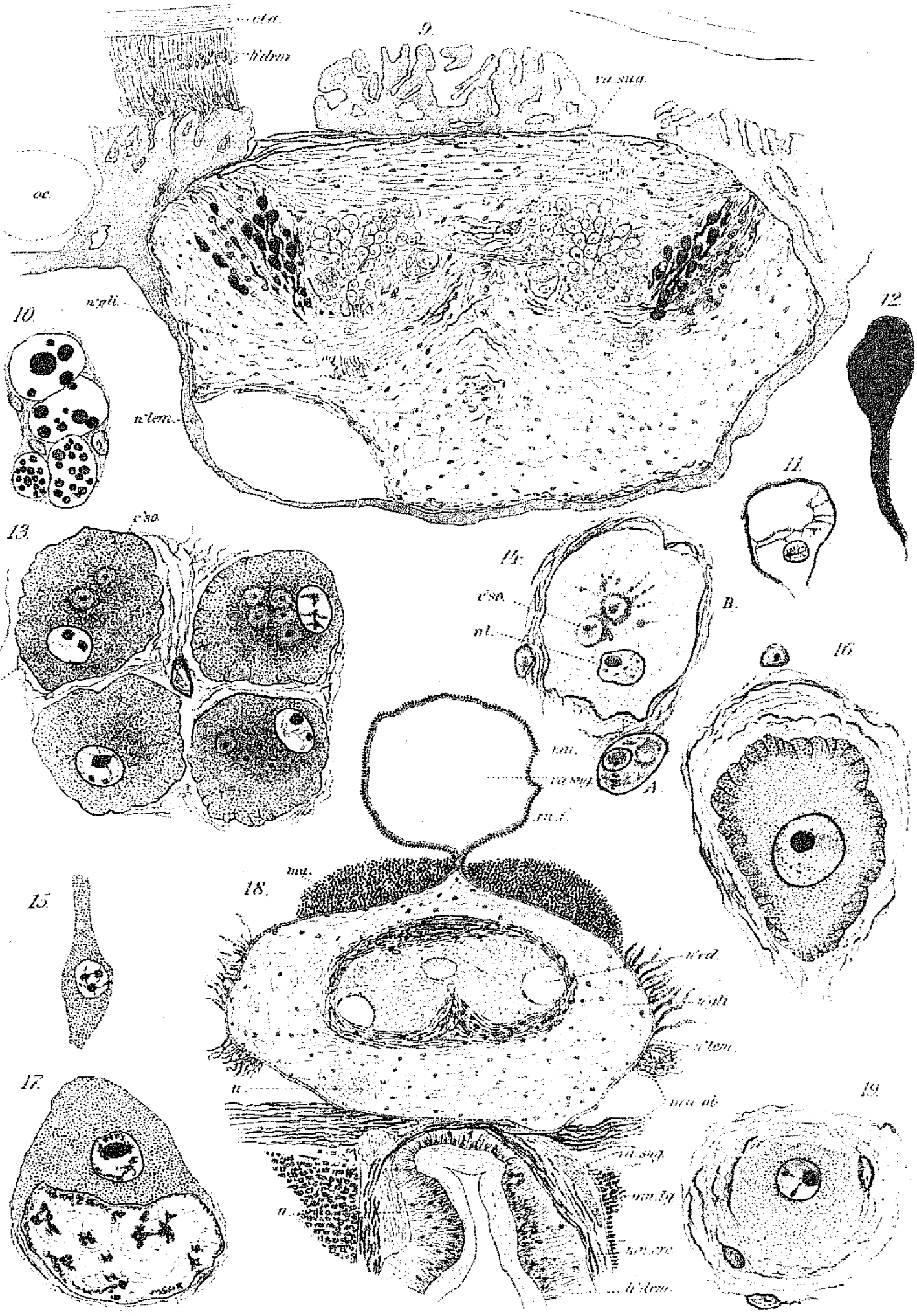
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PLATE 3.

Fig. 20. Parasagittal section of the cephalic segment tangent to the lateral surface of the posterior eye, to show the ciliated groove.

Fig. 21. Enlarged view of part of Figure 24, to show the arrangement of the nuclei of the "mushroom body."

Figs. 22 and 23. Para-sagittal sections of fibre *A* (compare Fig. 27), showing relation to fibres *B*, and also contact of fibres *B* with each other. The median giant fibre also appears in Fig. 23.

Fig. 24. Transverse section through the anterior part of the brain, showing the "mushroom body."

Fig. 25 is omitted.

Fig. 26. Frontal section of a longitudinal connective.

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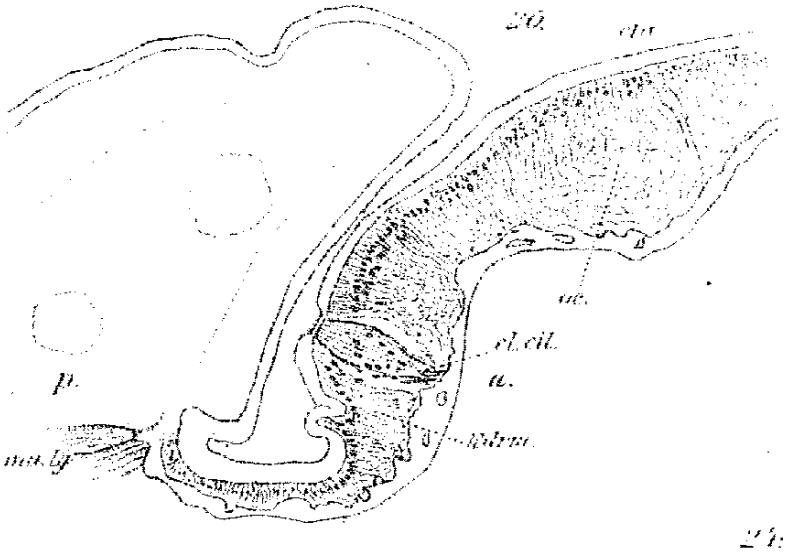

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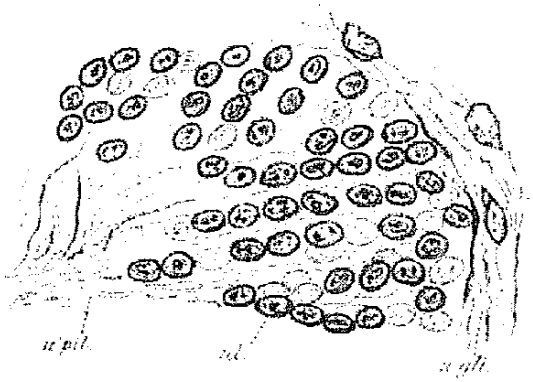

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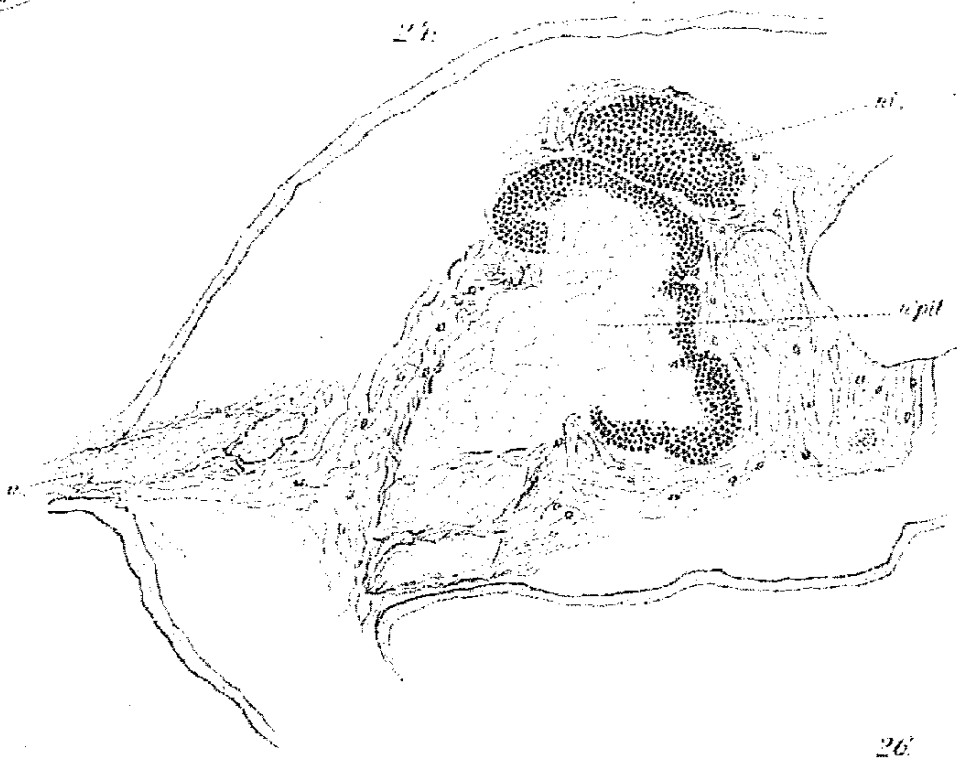

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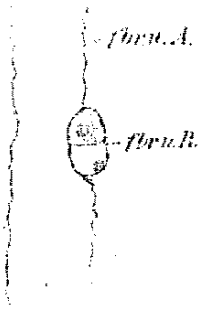

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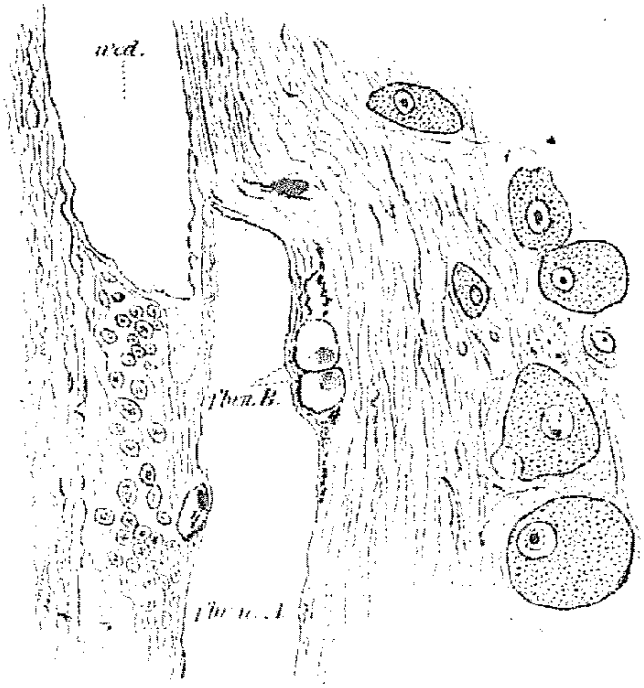

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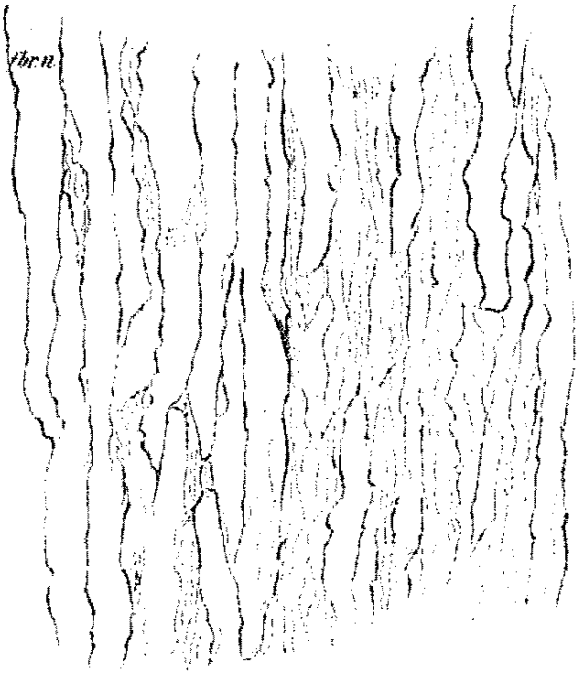


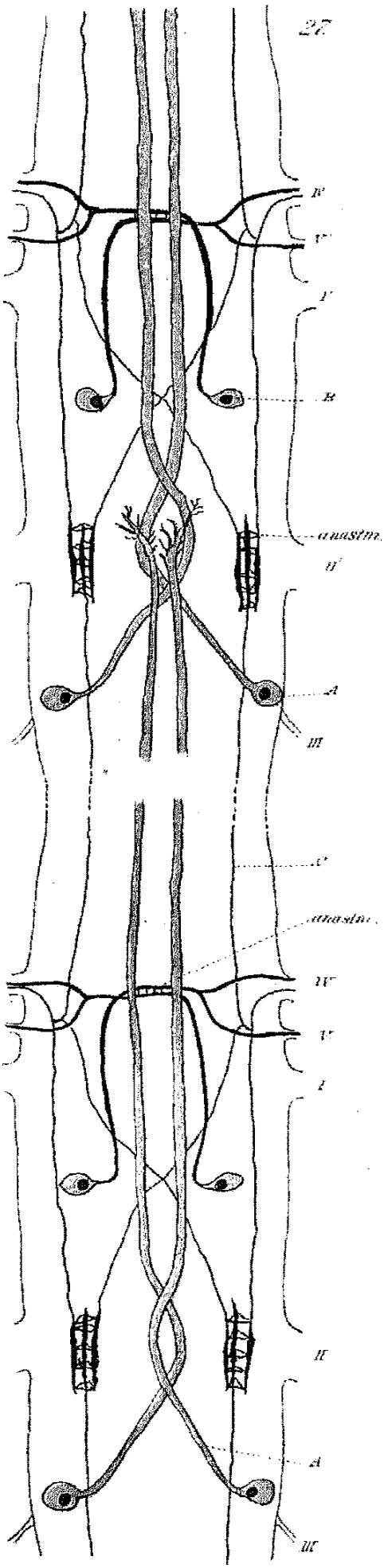
PLATE 4.

Fig. 27. Diagram to illustrate the fibre systems of sets *A*, *B*, and *C*, in two successive ganglia, as projected on the frontal plane.

Fig. 28. A pair of anastomosing fibres of set *B*.

Fig. 29. Fibres of set *C*, showing anastomosis between a posterior and a decussating branch.

Fig. 30. Fibres of set *C*, showing anastomosis between an anterior and a posterior branch.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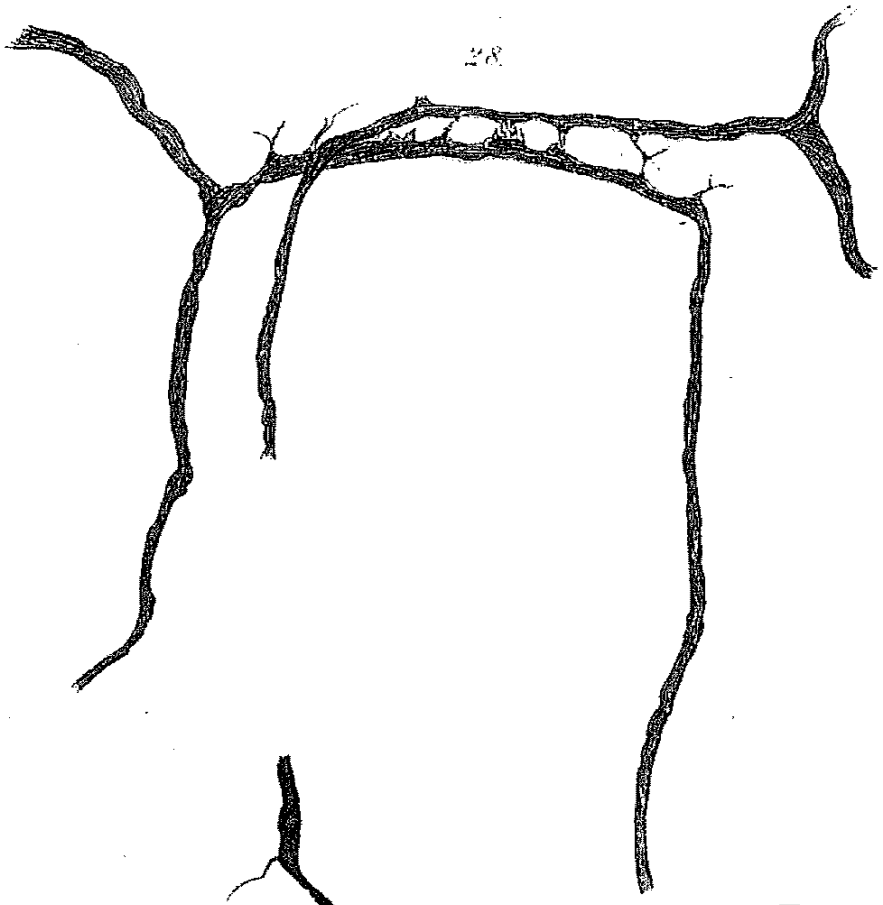
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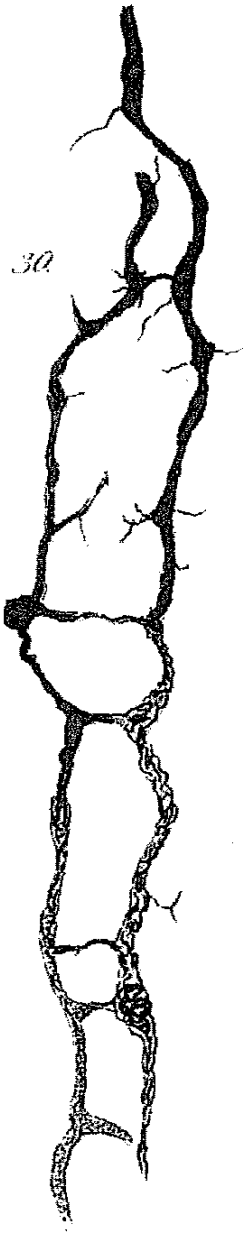
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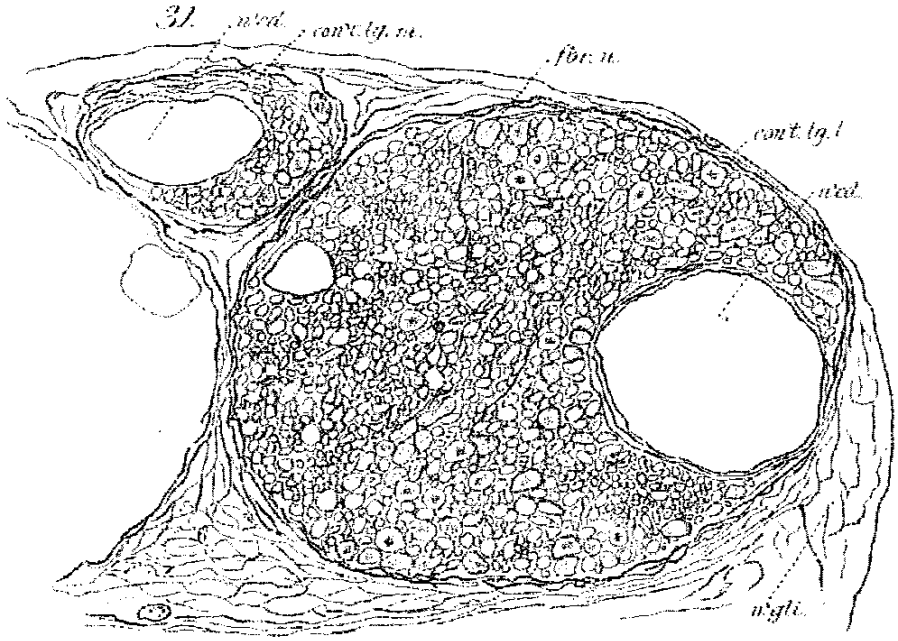
PLATE 5.

Fig. 31. Transverse section of the longitudinal connectives of the ventral cord.
Fig. 32. Frontal section of the ventral ramus of a parapodium (compare Fig. 8), showing motor (?) elements in the posterior branch of the second parapodial nerve.
Fig. 33. A section similar to that in Figure 32, showing sensory elements in the second parapodial nerve.
Fig. 34. Motor fibres and endings in the longitudinal muscles.
Fig. 35. Sensory cell from the base of a parapodium.
Fig. 36. Sensory cell from the side of the body near the fourth segmental nerve.
Fig. 37. Sensory nerve termination from the anterior wall of the parapodium.
Fig. 38. Sensory cell from the posterior wall of the parapodium.
Fig. 39. Diagram to show the course of fibres in the parapodial ganglion.
Fig. 40. Fibres of the "sub-hypodermal plexus" ending among the glands of the hypodermis.
Fig. 41. A nerve fibre showing the spiral arrangement of the fibrillæ, and also the shrinking of the axis cylinder from its sheath.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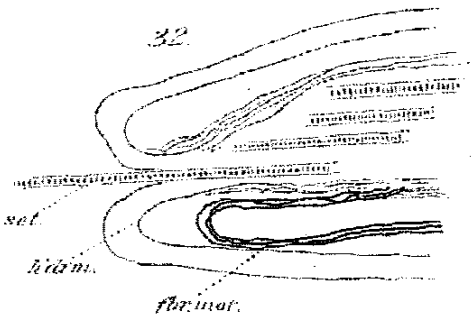
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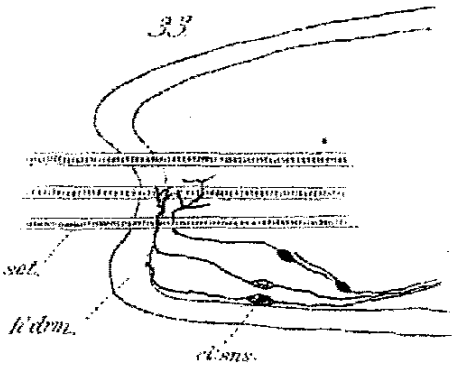
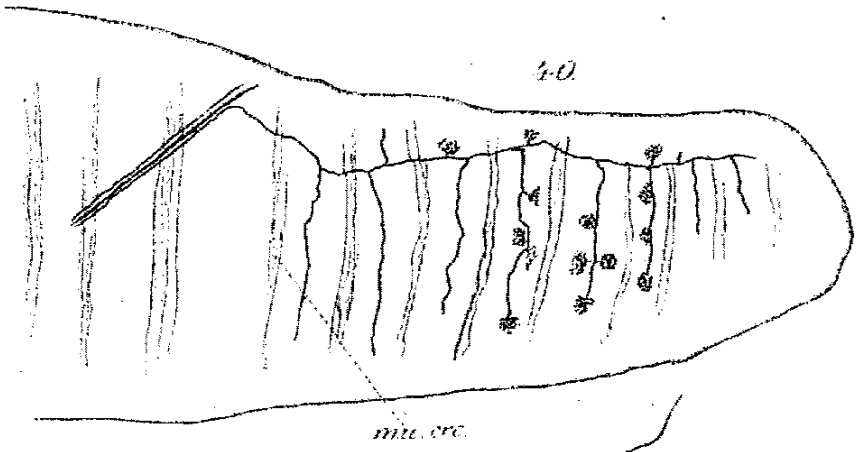
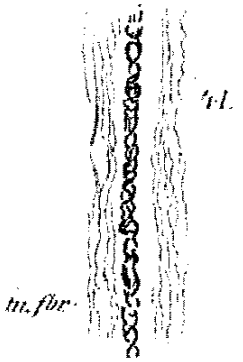
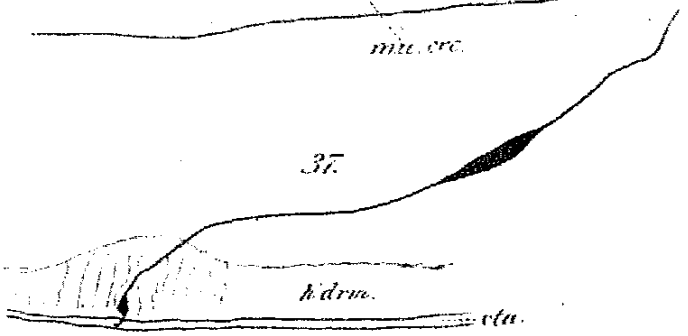
hdrm.
fbr. mar.

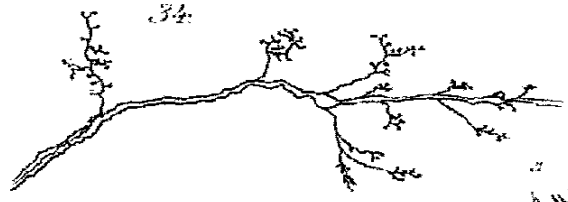

33.
set.
hdrm.
cl. sns.


40.
mu. crc.


41.
tn. fbr.


37.
hdrm.
cta.


38.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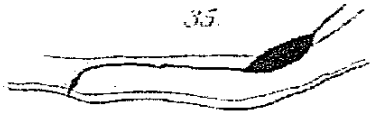
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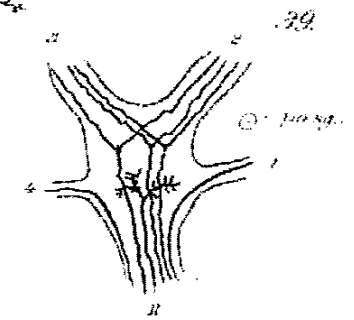
39.
a
e
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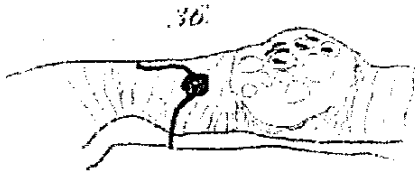
R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